Volume 095
Article 02

FISHERY RESEARCH

University of Idaho

THE EFFECT OF GROWTH RATE ON THE MATURATION SCHEDULE OF KOKANEE, ONCORHYNCHUS NERKA

By:

Scott D. Patterson
James Congleton
Dennis Scarnecchia

University of Idaho
Moscow, Idaho 83843

IDFG 94-24
August 1994

THE EFFECT OF GROWTH RATE ON THE MATURATION SCHEDULE OF KOKANEE, *ONCORHYNCHUS NERKA*

Project F-73-R-16

Subproject VI, Study IX

Research Progress Report-1993
Scott D. Patterson
Graduate Research Assistant
James Congleton and Dennis Scarnecchia
Principal Researchers

Department of Fish and Wildlife Resources
College of Forestry, Wildlife and Range Sciences
University of Idaho
Moscow, Idaho 83843

TABLE OF CONTENTS

TABLE OF CONTENTS (Cont.)

LIST OF TABLES

LIST OF FIGURES

CONTENTS

Page

CONTENTS

INTRODUCTION

Understanding the factors affecting age at maturity is essential for effective management of kokanee Oncorhynchus nerka in Idaho's lakes. The maturation schedule of kokanee, which directly affects the number and size of fish available for harvest, is influenced by genetic and physical environmental factors, and also by fish population densities, stocking rates, growth rates of fry (wild and hatchery-reared), and harvest rates.

Genetic and environmental factors interact to influence the age at sexual maturity of salmonids such as kokanee (Ricker 1972; Gardner 1976). Early maturing fish, i.e. those sexually mature one or more years before the majority of the age class, have been shown to produce a significantly higher proportion of early maturing progeny in Atlantic salmon Salmo salar (Thorpe et al. 1983; Glebe and Saunders 1986) and coho salmon O. kisutch (Iwamoto et al. 1984).

A higher proportion of early maturing fish has been reported in several studies when growth rate increased as a result of high feeding ration (reported by Crandell and Gall 1993) and higher temperature (Saunders et al. 1983). Thorpe (1986) reported evidence that increased growth rates decreased age at maturity for many salmonid species, including kokanee. Although age at maturity is heritable (Naeval 1983) and influenced by genetic factors (Bailey et al. 1980; Thorpe et al. 1980; Sutterlin and MacLean 1984), environmental conditions influence phenotypic expression of that trait. An individual fish's developmental history, therefore, is influenced by interacting genetic and environmental factors that in turn affect age at maturity and the fish's ultimate size (Scarnecchia 1983).

Although age at sexual maturity is influenced by genetic and environmental factors, the physiological processes involving the initiation and completion of sexual maturation are poorly understood. It is known that photoperiod and, to a lesser degree, temperature have important regulatory roles in controlling the completion of sexual maturation (reviewed by Lam 1983). Dustin and Saunders (1992) suggest that the commencement of sexual maturation in Atlantic salmon occurred during increasing day lengths and modelled the maturation "decision period" around the apex of the longest days (summer solstice in the northern hemisphere) and the completion of sexual maturation on decreasing day lengths.

The regulatory role of environmental factors in the initiation of maturation is not well understood. The time when outward physiological changes become manifest may be later than when the physiological decision to mature was actually made. In Thorpe's (1986) review, he concluded that instantaneous growth rate in spring was important for maturation and hypothesized "that salmon are physiologically aware of their spring (increasing day length) growth-rate through their rate of acquisition of surplus energy, and hormone kinetics associated with its storage: that, provided this rate is above a genetically determined level in the early spring when fish are sensitive to photoperiod stimulation of their gonadotrophic hormone system, gonad maturation will be triggered and reallocation of energy resources to include maturation be set in train." Brett and Shelbourn (1975) reported first feeding fry showed the highest potential instantaneous growth. Thorpe's hypothesis, therefore, suggests that the physiological decision is made early in life. In contrast, Peterman (1985) reported variation in mean age at maturity among Bristol Bay stocks of sockeye salmon for fish of the same smolt class. His results suggest that the physiological decision to mature is not made early in life, but is influenced by events later in life, specifically early in their marine phase of their life cycle. Other studies suggest spring fat reserves influence age at maturity (Rowe et al. 1991) and social competitive interactions influence sexual maturation (Metcalfe 1991). Although the factors affecting initiation of sexual maturation are poorly known, it is generally

thought that once the physiological decision is made the maturation processes are irreversible in semelparous species.

Specific genetic and environmental factors initiating sexual maturation are unknown. Factors interacting and regulating sexual development in iteroparous species like Atlantic salmon may not control sexual development in semelparous species like kokanee. Sexual maturation in salmonids is energetically costly and a terminal process to kokanee. The maturation process would, presumably, be triggered only if a fish had attained an energy threshold that would result in viable gametes. It is likely, therefore, that the environment influences the rate of attaining energy thresholds and these energy thresholds are genetically controlled by successful reproduction.

In this paper we will develop criteria for staging gonads of kokanee using histological methods and analyze gonad development from three kokanee populations in Idaho. We intend to distinguish sexually maturing from immature kokanee and detect the initiation of sexual maturation. We assess initiation and progression of sexual maturation by histological evaluation of gonads, by developing a gonadosomatic index based on percent gonad weight to body weight, and by observing changes in visceral fat. We analyze otoliths to assess annual growth from six kokanee populations in Idaho. Finally, we test three growth hypotheses regarding the initiation of maturation.

GOAL

To influence age of maturity to provide more large kokanee.

OBJECTIVES

1. Develop histological staging criteria for kokanee gonads.

2. Distinguish sexually maturing from immature kokanee gonads.

3. Determine monthly changes in the gonadosomatic index for kokanee from Coeur d'Alene Lake.

4. Test three research hypotheses:
   a) The "physiological decision" to mature occurs during the first growing season (first 122 days of feeding) as age 0+ fish.
   b) The "physiological decision" to mature occurs during the second growing season as age 1+ fish.
   c) The "physiological decision" to mature occurs during the third growing season as age 2+ fish.

Idaho's Kokanee Fisheries

The kokanee or nonanadromous O. nerka provides fishing opportunity to Idaho's anglers. In 1987, a statewide survey reported nearly a fourth of Idaho's anglers fished 230,000 days for kokanee (Reid 1989). Many kokanee fisheries, however, show extreme fluctuations in population abundance and the quality of fishing. Lake Pend Oreille supported a sport and commercial harvest of 1,000,000 fish annually from 1951 to 1957 (Buss 1957), declining to 100,000 fish by 1987 (Bowles et al. 1987), then rebounding to 230,000 fish in 1991 (Paragamian et al.

1992). Coeur d'Alene Lake supported a sport harvest of 500,000 fish annually from 1979 to 1981 (Rieman and Myers 1990; Mauser and Horner 1982) before declining to 164,000 fish in 1986 (Horner et al. 1987). Estimates of kokanee harvest from Spirit Lake have ranged from 59,000 fish in 1981 to 102,000 fish in 1992 (Nelson 1994, in preparation). Estimates of annual kokanee harvest from Dworshak Reservoir have ranged from 200,000 fish in 1988 to 100,000 fish in 1990 (Maiolie et al. 1991). In Priest Lake, the kokanee harvest declined from nearly 100,000 fish annually in the 1960s to only a few fish by 1975, when Idaho's record fish (3.15 kg) was caught. The numbers of kokanee adults trapped in Deadwood Reservoir increased from 120 fish in 1986 to 35,400 fish in 1993, but mean size decreased from 36 cm in 1986 to 21 cm in 1992 (Lowell 1993).

Since kokanee are semelparous (spawn once and die) and typically small (<30 cm), a quality kokanee fishery is predicated on size and abundance. A quality fishery for kokanee requires that maturation be delayed until fish are of sufficient size (at least 20 cm) to be available to anglers. Vulnerability to anglers increases with increasing size (Rieman and Myers 1990). Kokanee large enough to support a quality fishery are typically 25 cm in length maturing at two, three, or four years of age. Instability in the fishery may result from changes in maturation schedules.

Idaho fishery biologists request 15 to 20 million kokanee fry annually for stocking in numerous lakes and reservoirs. Hatchery managers have become concerned about the influence of factors, such as growth rate and rearing density, on kokanee age at maturity. Understanding the effects of hatchery rearing practices on maturation schedules is essential for effective supplementation of kokanee stocks with hatchery-reared fry.

METHODS

The first step is to age and determine the gonadal development stage of kokanee collected in Coeur d'Alene Lake, Dworshak Reservoir, and Lake Pend Oreille. The second step is to determine when the transition of immature to mature can be detected. The third step is to determine the effects of growth rates, age 0+, age 1+, and age 2+, on hatchery-reared kokanee and annual growth rates of six natural kokanee populations, on maturation schedules.

Natural Populations

Kokanee were sampled from six populations selected to provide a range in size and age at maturity: one lake with primarily age 4 spawners, Pend Oreille; three lakes with primarily age 2 and age 3 spawners, Coeur d'Alene, Deadwood and Payette; and two lakes with primarily age 1 and age 2 spawners, Dworshak and Spirit.

From May to October 1992 and March to October 1993, monthly samples of kokanee from age classes one, two, and three were collected from Coeur d'Alene Lake. The standard sample size for each age class was 25 fish. In July 1992 and 1993, fish from age classes 1 and 2 were collected from Dworshak Reservoir. In September 1992 and 1993, fish from age classes 1, 2, 3, and 4 were collected from Lake Pend Oreille. We captured fish with a mid-water trawl, measured their fork lengths to the nearest millimeter, weighed them to the nearest gram, and tentatively assigned them to age classes based on length. We surgically removed both gonads and fixed them in either 10% buffered formalin or Bouin's solution. Gonads were weighed to the nearest milligram in the lab after blotting dry. The fish's otoliths (sagittae) were removed for aging. Visceral fat of each fish was

estimated in 1993 using a modified categorical rating of visceral fat (Goede 1993) (Table 3).

In September 1992 and 1993, spawning kokanee were collected from Payette Lake, Spirit Lake (1993 only), and Deadwood Reservoir. Fork length and total lengths were measured and otoliths removed for aging.

Histological Procedures

Following fixation and weighing, gonads were trimmed, oriented, dehydrated in alcohol, and infiltrated with paraffin. Longitudinal sections were cut from gonads less than 1.0 g; transverse sections were cut from the anterior portion of larger gonads (greater than 1.0 g). Sections were cut six to eight um in thickness and stained with hematoxylin and eosin (H & E).

Stained sections were studied using a compound microscope at powers ranging from 40x to 450x. The separation of ovarian development stages (Table 1) was based on the cellular structure and staining characteristics of the most advanced oocyte observed (Yamamato et al. 1959; van den Hurk and Peute 1979; Wallace and Selman 1981; Nagahama 1983; Ng and Idler 1983). The separation of testes development stage (Table 2) was based on cellular structure and staining characteristics.

Gonadosomatic Index and Condition Factor

The gonadosomatic index (GSI) was calculated as:

$$GSI = (\text{gonad weight} / \text{body weight}) \times 100$$

Condition factor (K) was estimated as:

$$K = L^3 / W$$

where L = fish length in millimeters (mm)

w = fish weight in grams (g)

Aging and Back-Calculation of Growth

We aged fish by counting the number of annuli on the sagittal otolith. Otolith measurements and annuli enumeration (aging) were performed using the Optical Pattern Recognition System (OPRS). The OPRS measures light luminosity delineating opaque (summer growth) and translucent (winter growth) zones, displays the degree of luminescence on a Video Graphic Adapter (VGA) monitor, and displays the otolith image on a second monitor. Measurements along a selected radius are taken with a digital pad and mouse.

Fish length at each age was back-calculated by measuring the linear distance (radius) from the sulcus nucleus of the otolith to each annulus. This linear radius was 25° plus or minus 5° from the sulcus acusticus radius. The length at *n* years was calculated using the Fraser-Lee formula:

$$Ln\ a + (L - a)\ (V_{\circ})\ /\ (V,)$$

where L. = fish length at n years

a = 20 mm (estimated by approximation length of fish at otolith formation)

L = fish length at time of capture

V, = otolith radius distance from the sulcus nucleus to the nth annulus

V, = *otolith radius from the sulcus nucleus to otolith edge*

From these back-calculations of length at each age annual growth rates were determined.

Back-calculated lengths were verified by comparison with age-length relationship of fish collected in 1992 and 1993.

Hatchery Populations

To determine the effects of growth on the incidence of maturation, three experiments were conducted using Lake Pend Oreille kokanee reared at three Idaho Department of Fish and Game fish hatcheries (Cabinet Gorge, Clark Fork, and Sandpoint). For Experiment One, growth rates were manipulated March through July 1992 during the first year (age 0+) of life; slow growth, intermediate growth, or fast growth. For Experiment Two, growth rates were manipulated June 1992 through January 1993 during the second year (age 1+) year of life; slow growth or fast growth. For Experiment Three, growth rates were manipulated May through December 1993 during the third year (2+); slow growth or fast growth.

Experiment One (Age O+)

To test the research hypothesis that the "physiological decision" to mature occurs during the first growing season (the first 122 days of life) as age 0+ fish, growth rates of six groups of 2,000 fish each were manipulated by controlling water temperatures and feeding regimes. Two groups of fry were reared at Sandpoint Hatchery on a slow growth schedule at 7°C with intermittent feeding. Two groups of fry were reared at Clark Fork Hatchery on an intermediate growth schedule with natural water temperatures (seasonal and daily fluxes; minimum temperature 5°C and maximum temperature 12°C) and received full ration. Two groups of fry were reared at Cabinet Gorge Hatchery on a fast growth schedule at 11°C and received full ration. Fish were raised under similar densities, flow indices (Piper 1970), and diets. Each growth group was replicated. Fish were started on feed March 9, 1992.

After 122 days of rearing (July 17, 1992), 1,000 fish from each group were fin-clipped and the fish consolidated into two (1,187-liter) containers at Clark Fork Hatchery. Fish from the three rearing groups were identified by fin clips: no fin removal (slow growth), right ventral fin removal (intermediate growth), and left ventral fin removal (fast growth). Each container was loaded with 1,000 fish from each of the three groups. Excess fish were released. The fry were reared under natural temperatures and photoperiod (minimum winter water temperature 3°C and maximum summer temperature 17°C). To determine growth rates, 30 fish per rearing group from each of the replicated tanks were measured monthly.

An epizootic of Bacterial Kidney Disease (BKD) occurred in fish in both Clark Fork Hatchery containers in June 1993. Medicated (91.77 mg erythromycin per kilogram body weight) feed treatment began July 16 and continued for 25 days. We estimated 13% and 17% of the fish died of BKD, respectively, in the two containers. Mortality was similar in each group.

Experiment Two (Acre 1+)

To test the research hypothesis that the "physiological decision" to mature occurs during the second growing season as age 1+ fish, growth rates groups were manipulated. Fish were reared identically from mid-March 1992 until June 15, 1993 when growth rates were manipulated at Cabinet Gorge Hatchery by feeding regimes: four groups of 12,500 fish each were reared on a fast growth schedule and fed full ration, and two groups of 1,000 fish each were reared on a slow growth schedule and fed intermittently. Intermittent feeding schedules were one week on full ration and three weeks off ration. All groups were reared below 0.5 density index and 1.0 flow index (Piper 1970) at 10°C to 12°C. The slow growth groups were then transferred in January 1994 to Sandpoint Hatchery and switched to full ration. The fast growth groups remained at Cabinet Gorge Hatchery and continued to be reared on full ration. A standard 30-fish sample from each group was measured monthly and their condition factor estimated.

Fish in all six containers were infected with BKD, but the fish were not treated. The epizootic began in August 1993 and is still apparent. Losses up to February 1, 1994 were estimated at 42% in fast growth groups and 65% in the slow growth groups. Fish with clinical signs of BKD (bloated body, body fluids, kidney lesions) were not examined.

Experiment Three-Acre 2+

To test the research hypothesis that the "physiological decision" to mature occurs during the third growing season as age 2+ fish, fry 50 to 70 mm in length were obtained from Cabinet Gorge Hatchery in July 1991. Fish were reared identically from mid-March 1991 until May 1, 1993 when growth rates of four groups of fish were manipulated by feeding regimes. Two groups of fish with 198 fish and 190 fish, respectively, were reared on a fast growth schedule (full ration, 1% daily). Two groups of fish with 183 fish and 191 fish, respectively, were reared on a slow growth schedule (intermittent ration, 1% daily for the first seven days of the month and nothing the rest of the month). All groups were reared below 0.5 density index and 1.0 flow index (Piper 1970) at 7°C. A standard 30-fish sample from each group was measured monthly and their condition factor estimated. Feeding stopped November 1, 1993.

Ripe fish were spawned in November and December 1993. Eggs were measured and enumerated. Immature fish (not spawned) were killed and sexed.

Analysis

Statistical Methods

For Experiment One, the null hypothesis was that the physiological decision to mature did not occur during the first growing season (first 122 days of feeding) as age 0+ fish. The research hypothesis was that the physiological

decision to mature occurs during the first growing season (first 122 days of feeding) as age 0+ fish. For Experiment Two, the null hypothesis was that the physiological decision to mature did not occur during the second growing season as age 1+ fish. The research hypothesis was that the physiological decision to mature occurs during the second growing season as age 1+ fish. For Experiment Three, the null hypothesis was that the physiological decision to mature did not occur during the second growing season as age 2+ fish. The research hypothesis was that the physiological decision to mature occurs during the third growing season as age 2+ fish. We tested the experiments based on analysis of variance (ANOVA) and pairwise multiple t-tests at the 0.05 significant level.

Differences in egg size, total egg weight, fecundity, and fish size were tested with 2,500 random (Monte Carlo) permutations for sample size less than 30, and t-test for sample sizes 30 or greater at 0.05 significance level.

RESULTS AND DISCUSSION

Aging Validation

The observed lengths from the 1990, 1991, and 1992 cohorts were comparable to their back-calculated lengths (Figures 1, 2, 3), and the 1990 cohort's back-calculated lengths were similar when sampled in 1992 or 1993 (Figure 4). In Figure 3, the back-calculated mean length is above that observed in the growth curve, but the two standard errors (SE) around the back-calculated mean does encompass the observed mean length. Biological factors, such as natality, predation, emigration, and/or sampling bias could cause this slight discrepancy.

The time of annulus formation on the otolith varied between individual kokanee. We detected the start of its formation in older fish as early as October 29, 1992 (the last sample date of the year), but the annulus was not completely formed around the periphery. When sampling resumed in late winter (March 17, 1993), annulus formation was complete in about 70% of the fish. Annulus formation was complete in almost all fish (84/85) by April 23, 1993. April 1 has, therefore, been set as the date of annulus formation and the date that back-calculated lengths are associated with.

Our results suggest the Fraser-Lee equation is a reasonable estimate of back-calculated fish lengths (Figures 1, 2, 3, and 4). Although numerous other methods can be used to back-calculate length (reviewed by Carlander 1981; Francis 1990; Ricker 1992), our results indicate the Fraser-Lee equation provides an adequate estimate for this study.

Gonadal Development

Gametogenesis in fish follows the general vertebrate pattern. Kokanee ovaries develop through a sequence of mitotic proliferation, meiotic divisions, primary oocyte growth, cortical alveoli formation, vitellogenesis, and maturation (Wallace and Selman 1981; Wallace et al. 1986). Similarly, kokanee testes develop by mitotic proliferation and meiotic division. Female kokanee commence oogenesis early in life and male kokanee commence spermatogenesis late in life.

In most tetrapods, gonadal development is regulated by two pituitary gonadotropins (GTHs): luteinizing hormone (LH) and follicle-stimulating hormone (FSH). Although regulation of fish reproduction by one or two GTHs has been controversial, Swanson et al. (1990) isolated GTH I (analogous to LH) and GTH II (analogous to FSH) from pituitaries of spawning coho salmon. Furthermore, the

results of Yan et al. (1992) indicated distinct receptors for salmon gonadotropins I and II in thecal and granulosa cells of coho salmon ovaries. These findings indicate that the hypothalamus-gonadal axis functions in teleosts in much the same way as in other vertebrate animals.

Description of Oocyte Development

Stage One

Although stage one oocytes were not observed in the present study, they have been described in capelin by Forberg (1981). Stage-one oocytes are formed in small clusters. The nucleus occupies 75% of the total diameter. The cytoplasm is weakly basophilic while the nucleus is more basophilic. Bromage and Cumaranatunga (1987) reported that oogonial (Stage 1) oocytes, found in rainbow trout 0 and 90 days post-fertilization, were in the synaptic leptotene prophase of meiotic division.

Stage Two

Stage two oocytes are characterized by basophilic staining of cytoplasm and nucleus. Weak or strong staining may be an artifact of preservation; however, the nucleus is typically a darker blue than the cytoplasm. The nucleus is round with several perinucleoli (dark stained) in or on its periphery. The follicle layer (theca) consists of squamous-type cells. Mesentery tissue is found between oocytes (ova), and ova still occur in clusters.

Stage Three

Stage three oocytes are characterized by basophilic staining of cytoplasm and nucleus. The nucleus is round with several perinucleoli (dark stained) in or on its periphery. Some ova have a "lacy" appearance which may be an artifact of preservation or cytoplasmic organelles. Non-staining vacuoles appear in the cytoplasm and increase in number and may develop nuclear-like centers (cortical alveoli) as the fish progress through this stage. The follicle layer (theca) consists of squamous-type cells. Bromage and Cumaranatunga (1987) reported rainbow trout in diplotene prophase of meiotic divisions. Russell (1992) reports tetrapod ova in diplotene prophase remain resting in this stage until the onset of puberty.

Stage Four

Stage four oocytes are characterized by basophilic cytoplasm and a weak acidophilic (light red or purple) irregular shaped nucleus. Balinsky (1970) suggested the irregular nuclear shape is caused by the transportation of RNA into the cytoplasm used in the building of yolk. Several perinucleoli persists on the periphery of the irregular outline of the nucleus. Numerous cortical alveoli (non-staining vacuoles) fills the cytoplasm. The follicle layer starts differentiation into thecal and granulosa layers. Russell (1992) suggested the irregular nuclear shape is a progression into the diakinesis stage of meiosis. The diakinesis stage is followed by more rapid progression of the remaining (metaphase, anaphase, telophase) meiotic divisions.

Stage Five

Stage five oocytes are characterized by the zona radiata, an acidophilic staining membrane on the periphery of the cytoplasm. The cytoplasm becomes less basophilic and cortical alveoli (non-staining vacuoles) nearly fills the cytoplasm. The irregular shaped nucleus becomes more acidophilic. Several perinucleoli persist on the periphery of the irregular outline of the nucleus. The follicle layer continues differentiation into follicle thecal and granulosa layers.

Stage Six

Stage six oocytes are characterized by distinct thecal and granulosa follicle layers. The granulosa layer consists of cuboidal cells that appear between the zona radiata and theca. The cytoplasm becomes less basophilic and cortical alveoli (non-staining vacuoles) nearly fill the cytoplasm. The irregular shaped nucleus becomes more acidophilic. Several perinucleoli persists on the periphery of the irregular outline of the nucleus. The zona radiata widens and contains distinct radial striations. Balinsky (1970) showed such striation to be pore through which cytoplasmic microvilli penetrate for metabolic exchange between follicle layer(s) and oocyte.

Stage Seven

Stage seven oocytes are characterized by acidophilic fat globules in the cytoplasm. The thecal and granulosa layers are distinct. The cortical alveoli (non-staining vacuoles) disappear in late stage-seven fish. Several perinucleoli persists on the periphery of the irregular outline of the nucleus.

Stage Eight

Stage eight oocytes are characterized by migration of the nucleus toward the micropyle on the oocyte periphery. This stage was not detected in our study. It is easier to distinguish this stage using macroscopic techniques rather than histological ones (West 1990).

Atresia

Two types of atretic oocytes were detected. The first type, previtellogenic atresia (Type 1), includes oocytes not recruited into vitellogenic stages but remaining in stage three. The second type, postvitellogenic atresia (Type 2), includes oocytes recruited into vitellogenic stages but failing to mature. Ova undergoing Type 2 atresia were surrounded by many lymphocytes. Bromage and Cumaranatunga (1987) suggested that atresia is an important determinant of spawning fecundity. In poor environmental conditions, for example, a fish could physiologically sacrifice fecundity to assure viable gametes. The atretic process and reallocation of that energy would be important for successful reproduction. Some flexibility in the trade-off between fecundity and egg size would result.

Description of Testes Development

Stage One

Stage one testes are characterized by weak basophilic and acidophilic staining. Spermatogonia surrounded by thick connecting tissue form cysts. Round shaped spermatids are present but in low numbers.

Stage Two

Stage two testes are characterized by stronger staining characteristics and an increase in size. Lighter stained tissue surrounds darker, round spermatids appearing "donut" shaped. Late stage two is characterized by numerous spermatids.

Stage Three

Stage three testes are characterized by motile spermatozoa. Stage three testes were not detected in this study.

Natural Populations

Coeur d'Alene Lake

Analysis is not completed. The 1993 samples are summarized in Tables 4 and 5.

Similar tables summarizing data collected in 1992 will be completed by May 1994.

Gonadosomatic Index

Energy allocation changes when kokanee are maturing as energy resources are diverted from somatic to gonadal growth. We detected a change in gonadal growth by May of the spawning year in both male and female Coeur d'Alene Lake kokanee (Figures 7 and 8). Ovarian growth coincided with stages 5, 6 and 7 and testicular growth with stage 2.

Fat Index and Condition Factor

We detected a difference in energy reserve use between maturing and immature Coeur d'Alene Lake kokanee. The condition factor of immature kokanee (age 1+) increased from May through October 1992, but declined by late winter (March 17, 1993). During the winter period, fish weight declined with no visible visceral fat remaining by March; fish length increased during this period (Figure 5). In contrast, the condition factor of age 2 kokanee also increased during the May to October period, but remained the same through the winter with little

change in body weight or length (Figure 6). These fish, now age 3, retained their visceral fat, unlike the age 1 and age 2 fish.

Both age 1 fish and age 2 fish (immature) had little energy reserved in visceral fat by March 1993. Both age groups developed visceral fat reserves by October 1993 (Tables 4 and 5). In contrast, age 3 fish (stage 5) had energy reserved in visceral fat in March 1993. Energy reserves decreased by October, as energy was allocated into reproduction. Our results suggest a cyclic progress in visceral fat reserve. Acquisition of energy is apparently important for immature fish to survive through the winter; however, acquiring and retaining energy reserves for specific use is important to the maturation process. It is unknown whether retention of energy reserves through the winter causes maturation or maturation process causes retention of energy reserves.

Lake Pend Oreille

Analysis is not completed.

Dworshak Reservoir

Analysis is not completed.

Spirit Lake

Analysis is not completed.

Deadwood Reservoir

Analysis is not completed.

Payette Lake

Analysis is not completed.

Hatchery Populations

Experiment One-Age 0+

Experiment One has not been completed. We are unable to test the hypothesis that the physiological decision to mature occurs during the first growing season (the first 122 days of life) as age 0+ fish. The incidence of maturation will be based on Stage five ovaries and Stage two testes. Data collection and analysis will be completed in May 1994.

All three early rearing groups produced age 1 mature males in 1993. The significance of this has not been determined. No mature or maturing females were detected in 1993.

Size differences caused by the rearing treatments have persisted throughout the experiment. Fast early growth, therefore, supports a circular (cause or effect) argument resulting in two possible conclusions to rejection of the null hypothesis. First, high instantaneous growth during the first growing season initiates the maturation process producing a higher proportion of early maturing fish. Or secondly, faster growing fish obtain a certain size threshold earlier in life resulting in a higher proportion of early maturating fish.

Experiment Two-Age 1+

Experiment two has not been completed. We are unable to test the hypothesis that the physiological decision to mature occurs during the second growing season as age 1+ fish. The incidence of maturation will be based on Stage five ovaries and Stage two testes. Data collection and analysis will be completed in May 1994.

Experiment Three-Age 2+

In males, 65% and 57% matured in the two "fast" treatment replicates compared to 60% and 58% matured in the two "slow" treatment replicates. There was no significant difference in maturation among the four replicates ($p=0.56$). After collapsing into two treatments, "fast" and "slow," there was no significant difference between groups ($p=0.72$).

In females, 25% and 39% matured in the two "fast" treatment vats, and 39% and 43% matured in the two "slow" treatment vats. There was a significant difference among the four vats. Using multiple "t" comparisons, the "fast" treatment with 25% incidence of maturation is significantly different from the other three. Two scenarios could have caused this difference. The first is that fast growth retards maturation development. The second is that we loaded a disproportional number of immature females into that "fast" treatment vat. Since the first scenario contradicts extensive literature reviews, we support the second scenario.

We failed to reject the null hypothesis that the physiological decision to mature did not occur during the third growing season as age 2+ fish. We conclude that the physiological decision to mature occurs prior to the growing season preceding spawning and is irreversible after May 1 of the spawning year. Poor growth the summer preceding spawning significantly ($p<0.001$) reduced fish size, fecundity, egg size, and total egg weight (Table 6 and 7), but did not change the incidence of maturation.

Since female fish sampled in Coeur d'Alene Lake had progressed into Stage five and/or Stage six by April and May of the spawning year and male fish into Stage two, it seems likely these stages are good indicators of irreversible maturation process (Tables 4 and 5). The result of this experiment, therefore, allows us to use Stage five (females) and Stage two (males) as indicators of irreversible maturation process when analyzing experiments one and two.

Table 1. Ovary stages and distinguishing characteristics.

Stage	No.	Characteristics
Oogonia	1	Small nested oocyte.
Primary Oocyte	2	Germinal vesicle (nucleus) occupies most of the cell. Little ooplasm (cytoplasm).
Perinucleolus	3	Many nucleoli on germinal vesicle periphery. Non-staining vacoule appear, become more apparent and numerous around ooplasm periphery in larger fish. Thecal membrane squamous cell type.
Cortical Alveoli (Early)	4	Nucleus becomes more acidophilic and irregular shaped. "Nuclear-like" cortical alveoli[a] (non staining vacuoles, H&E) appear. Thecal membranes begins differentition to granulose (columnar cell type)
Zona Radiata (Late)	5	Striated zona radiata (red staining inner membrane) appears.
Oil Drop (Early Vitellogenesis)	6	Oil drops[b] (red-staining droplets H&E) appear. Yolk vesicles still apparent, filling most of ooplasm. Distinct thecal and granulosa membranes.
Yolk (Late Vitellogenesis)	7	Oil drops consolidate. Zona radiata thickens.
Migratory	8	Perinuclei disappear. Germinal vesicle migrates toward pole.

[a] referred to in literature as "yolk vesicle, yolk granules, yolk precursor, non staining vacuoles"

[b] referred to in literature as "fat vesicles, vacuoles or globules, fatty or lipid droplets, wine-staining vacuole, staining-yolk vesicle, yolk granule"

Table 2. Testes stage and distinguishing characteristics.

Stage	No	Characteristics
Primary Spermatogonia	1	Spermatogonia in cysts forms lumps. Thick layers of connecting tissue surround cells.
Secondary Spermatogonia	2	Cysts increase in size. Space in center forming "donut" shapes.
Spermatocyte	3	Appearance of spermatid and spermatozoa.

Table 3. Percent of pyloric caeca covered with visceral fat.

Percent	Categorical Number	Description
0 - 9	1	No fat between caeca.
10 - 49	2	Fat present between caeca but less than width of caeca.
50 - 89	3	Fat present between caeca and greater than the width of caeca.
90 - 100	4	Fat almost completely covering caeca

Table 4. Testicular stages and fat index of age 1, 2, and 3 male kokanee sampled from Coeur d'Alene Lake in 1993.

Age	Sample Date	Mean Fork Length in mm (SE)	Mean Weight in grams (SE)	Sample Size	Testes Stages		Fat Index			
					1	2	1	2	3	4
I	17 March	73 (5)	3.2 (0.8)	10	10		10			
I	23 April	73 (4)	3.2 (0.6)	10	10		10			
I	27 May	89 (6)	6.7 (1.5)	15	15		14	1		
I	1 July	108 (5)	12.8 (2.0)	12	12		3	9		
I	16 July	117 (13)	17.1 (4.7)	14	14		1	12	1	
*I	26 August									
I	20 September	144 (10)	31.0 (8.3)	12	12			8	4	
I	15 October	152 (10)	37.7 (8.0)	17	17			4	10	3
II	17 March	137 (7)	22.4 (4.3)	13	13					
II	23 April	140 (10)	23.8 (6.3)	15	15		9	4	1	1
II	27 May	139 (6)	25.6 (3.6)	12	12		12			
II	1 July	154 (6)	37.4 (4.0)	12	12			11	1	
II	16 July	164 (5)	47.2 (3.1)	20	20			18	2	
II	26 August	178 (5)	63.6 (5.8)	9	9				7	2
II	20 September	186 (13)	72.9 (16.1)	18	16	2		2	3	13
II	15 October	179 (7)	72.8 (7.6)	16	16					16
III	17 March	201 (8)	87.5 (9.7)	13	1	12				
III	23 April	205 (13)	91.2 (14.4)	3		3				4
III	27 May	211 (8)	95.5 (9.2)	12	2	10				12
III	1 July	217 (4)	107.8 (7.7)	5		5			2	3
III	16 July	209 (16)	98.4 (19.4)	15	8	7		3	7	5
III	26 August	215 (na)	125.0 (na)	1		1			1	
III	20 September	238 (16)	146.0 (25.8)	13	2	11	2	9		4
IV	17 March	206 (na)	108.8 (na)	1		1				
IV	23 April	212 (na)	92.7 (na)	1		1				1
IV	16 September	251 (23)	182.0 (53.2)	3		3		3		

* analysis not finished

Table 5. Ovarian stages and fat index for age 1, 2, and 3 female kokanee sampled from Coeur d'Alene Lake in 1993.

Age	Sample Date	Mean Fork Length in mm (SE)	Mean Weight in grams (SE)	Sample Size	Ovary Stages						Fat Index			
					2	3	4	5	6	7	1	2	3	4
I	17 March	72 (5)	3.2 (0.7)	11		11					11			
*I	23 April	75 (4)	3.5 (0.6)	14							14			
I	27 May	88 (6)	6.9 (1.3)	11	1	10					11			
I	1 July	109 (7)	12.8 (2.1)	7		7						7		
I	16 July	120 (5)	17.5 (2.5)	10		10						10		
*I	26 August													
I	20 September	142 (11)	32.3 (9.9)	14		14						4	7	3
I	15 October	149 (11)	35.4 (8.2)	10		10					1	2	7	
II	17 March	138 (9)	23.8 (4.7)	9		8		1						
*II	23 April	139 (8)	22.6 (4.4)	20							15	4	1	
II	27 May	138 (8)	26.3 (5.5)	22		21	1				19	4		
II	1 July	150 (8)	35.2 (4.7)	17		16	1					17		
II	16 July	166 (16)	51.2 (19.5)	12		10	1			1		11	1	
II	26 August	174 (4)	61.0 (4.8)	21		19	2						18	3
II	20 September	182 (16)	67.8 (20.4)	15		10	3	1		1		1	4	10
II	15 October	178 (4)	73.1 (4.7)	17		11	6							17
III	17 March	206 (9)	91.8 (11.7)	20			1	19						
III	23 April	203 (12)	82.7 (9.7)	7				7						7
III	27 May	206 (9)	93.8 (11.3)	13				1	12				6	7
III	1 July	217 (3)	104.5 (4.4)	7						7			3	4
III	16 July	207 (17)	95.7 (21.7)	9		1		3		5		3	3	3
III	20 September	240 (8)	145.0 (10.6)	12						12	1	11		
III	15 October	238 (10)	142.0 (15.0)	4						4	4			
IV	16 July	222 (na)	116.0 (na)	2						2	1	1		
IV	15 October	240 (na)	159.0 (na)	1						1	1			

* analysis not finished

Table 6. Effects of third summer growth rates on maturation schedules of kokanee males.

	Slow				Fast			
	Vat 7		Vat 18		Vat 8		Vat 17	
	Immature	Mature	Immature	Mature	Immature	Mature	Immature	Mature
Start: Number	45	63	41	62	41	76	40	52
Mortality	0	4	2	2	0	8	1	6
End: Number	45	59	39	60	41	68	39	46
Percent Mature	58.3		60.2		65.0		56.5	
Start: Mean Fork Length (cm)	23 (3)		23 (2)		23 (2)		23 (2)	
End: Mean Fork Length (cm)	24 (2)	27 (3)	23 (2)	26 (3)	29 (2)	34 (3)	30 (2)	32 (2)
Start: Mean Weight (g)	148 (41)		134 (36)		143 (37)		134 (40)	
Start: K-Factor (10^{-5})	1.126 (0.083)		1.146 (0.072)		1.140 (0.077)		1.121 (0.094)	
Sept. 29 1993 K-Factor (10^{-5})	1.021		1.013		1.237		1.200	
*End: Mean Weight (g)	141	201	123	178	302	486	324	393

* Weight estimated from K-factor (Piper 1970).
Number in parenthesis is one standard error.

Table 7. Effects of third summer growth rates on the maturation schedules of kokanee females.

	Slow				Fast			
	Vat 7		Vat 18		Vat 8		Vat 17	
	Immature	Mature	Immature	Mature	Immature	Mature	Immature	Mature
Start: Number	46	29	50	38	60	21	60	38
Mortality	0	2	0	1	0	2	2	3
End: Number	46	27	50	37	60	19	58	35
Percent Mature	38.7		43.2		25.9		38.8	
Start: Fork Length (cm)	23 (3)		23 (2)		23 (2)		23 (2)	
End: Fork Length (cm)	23 (2)	26 (2)	23 (2)	26 (2)	29 (3)	32 (2)	28 (3)	32 (2)
Start: Weight (g)	148 (41)		134 (36)		143 (37)		134 (40)	
Start K-Factor (10^{-5})	1.126 (0.083)		1.146 (0.072)		1.140 (0.077)		1.121 (0.094)	
Sept. 29 1993 K-Factor (10^{-5})	1.021		1.013		1.237		1.200	
*End Weight (g)	124	179	123	178	302	405	263	393
Total Egg Weight (g)		30.1 (8.5)		30.0 (8.2)		65.4 (9.9)		65.7 (12.6)
Egg Size (eggs/g)		23.6 (2.5)		24.0 (2.2)		19.4 (2.7)		20.0 (2.6)
Spawning Fecundity		686 (161)		708 (162)		1254 (156)		1314 (229)

* Weight estimated from K-factor (Piper 1970).
Number in parenthesis is one standard error.
There was no significant difference (randomization theory, 2500 permutations) between the two slow vats (7 and 18) for ovary weight ($P=0.81$), egg size ($P=0.88$), spawning fecundity ($P=0.71$), and no significant difference (randomization theory, 2500 permutations) between the two fast vats (17 and 8) for ovary weight ($P=0.95$), egg size ($P=0.36$), spawning fecundity ($P=0.54$). However, when the two slow vats where combined with each other and the two fast vats combined with each other, there was a significant difference (t-test) for ovary weight ($P<0.001$), egg size ($P<0.001$), and spawning fecundity ($P < 0.001$).

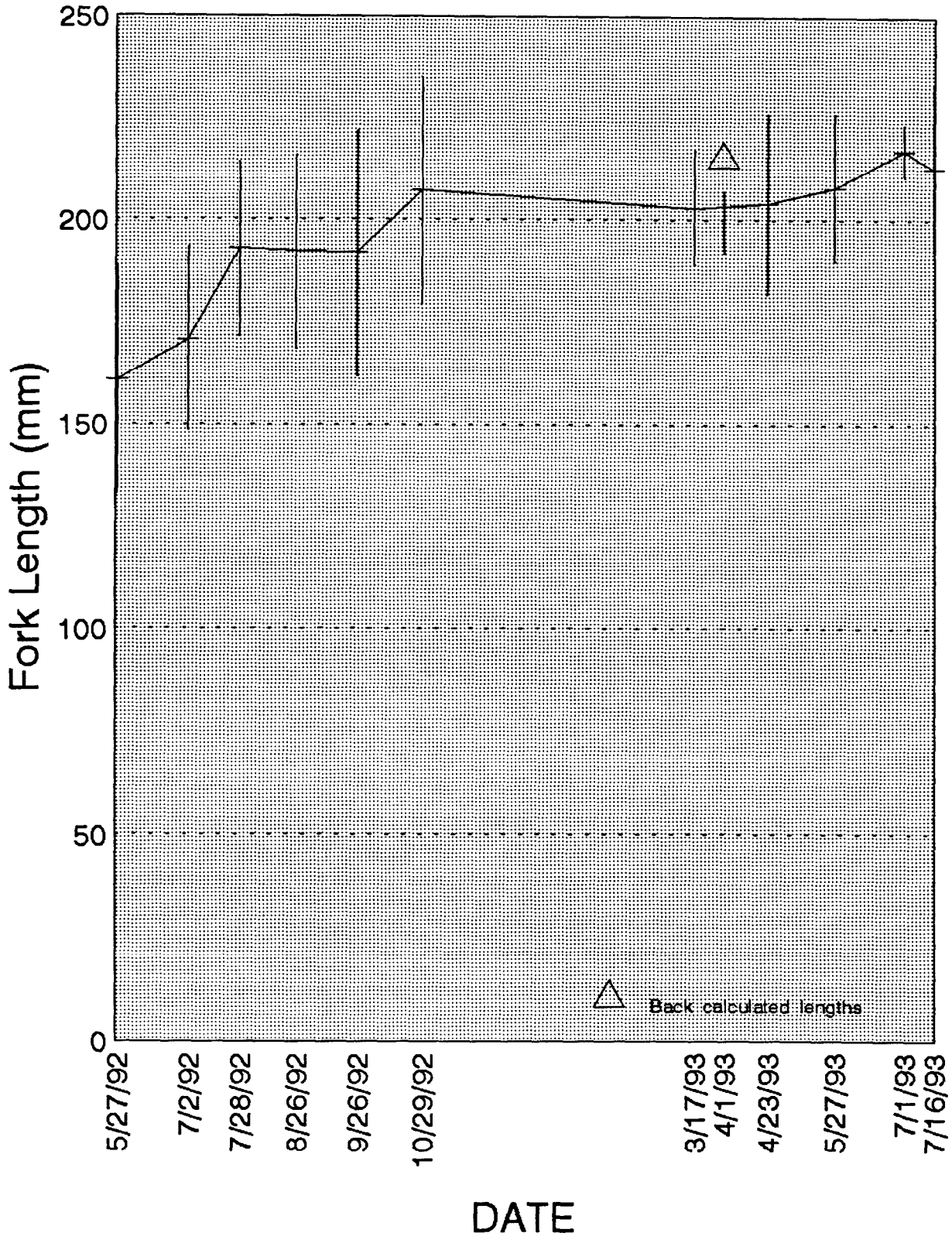

Figure 1. Observed growth curve for 1990 kokanee cohort (May 27, 1992 to July 16, 1993) plotted with back-calculated mean length from four sample dates (April 23, May 27, July 1, July 16) in 1993.

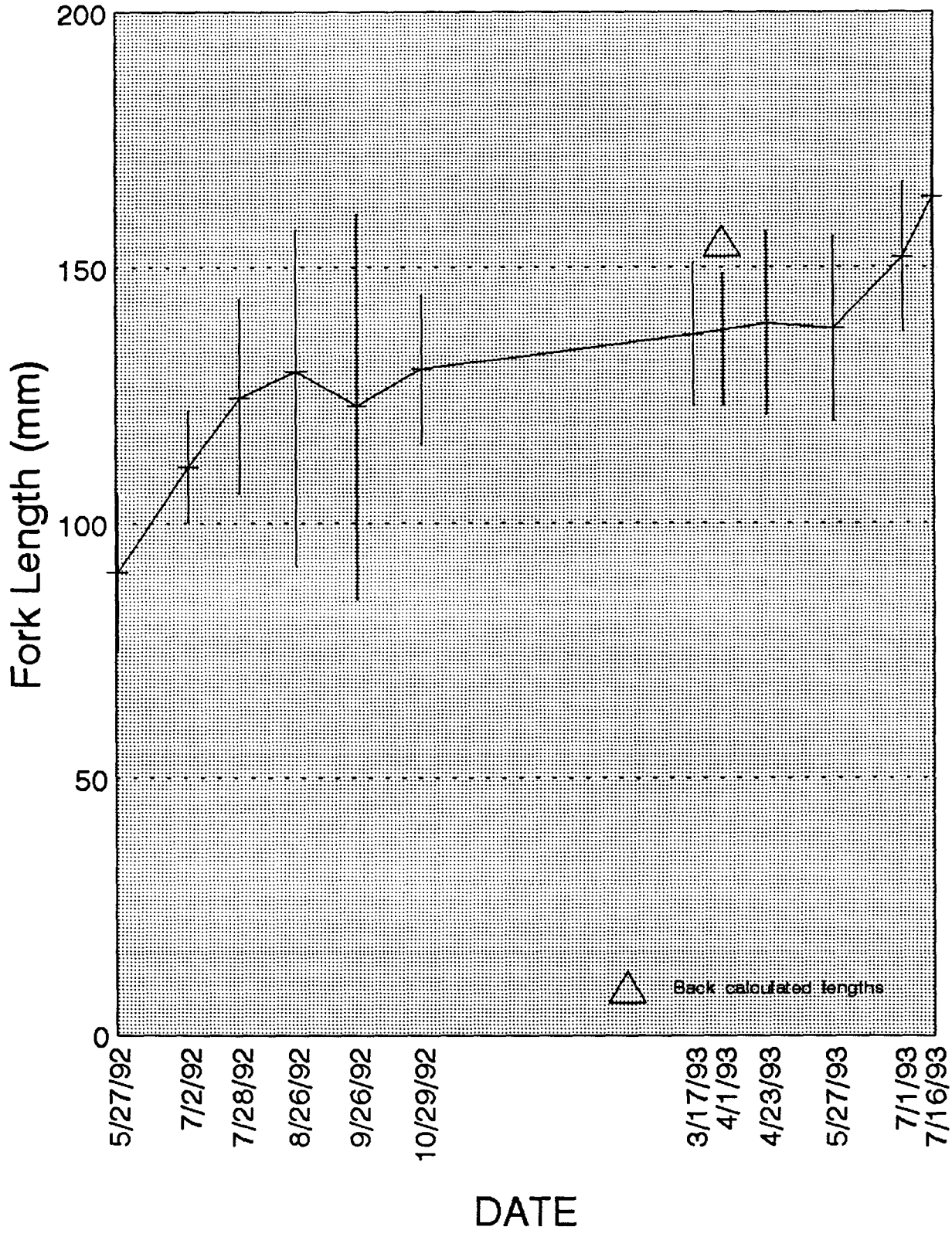

Figure 2. Observed growth curve for 1991 kokanee cohort (May 27, 1992 to July 16 1993) plotted with back calculated mean lengths from four sample dates (April 23, May 27, July 1, July 16) in 1993.

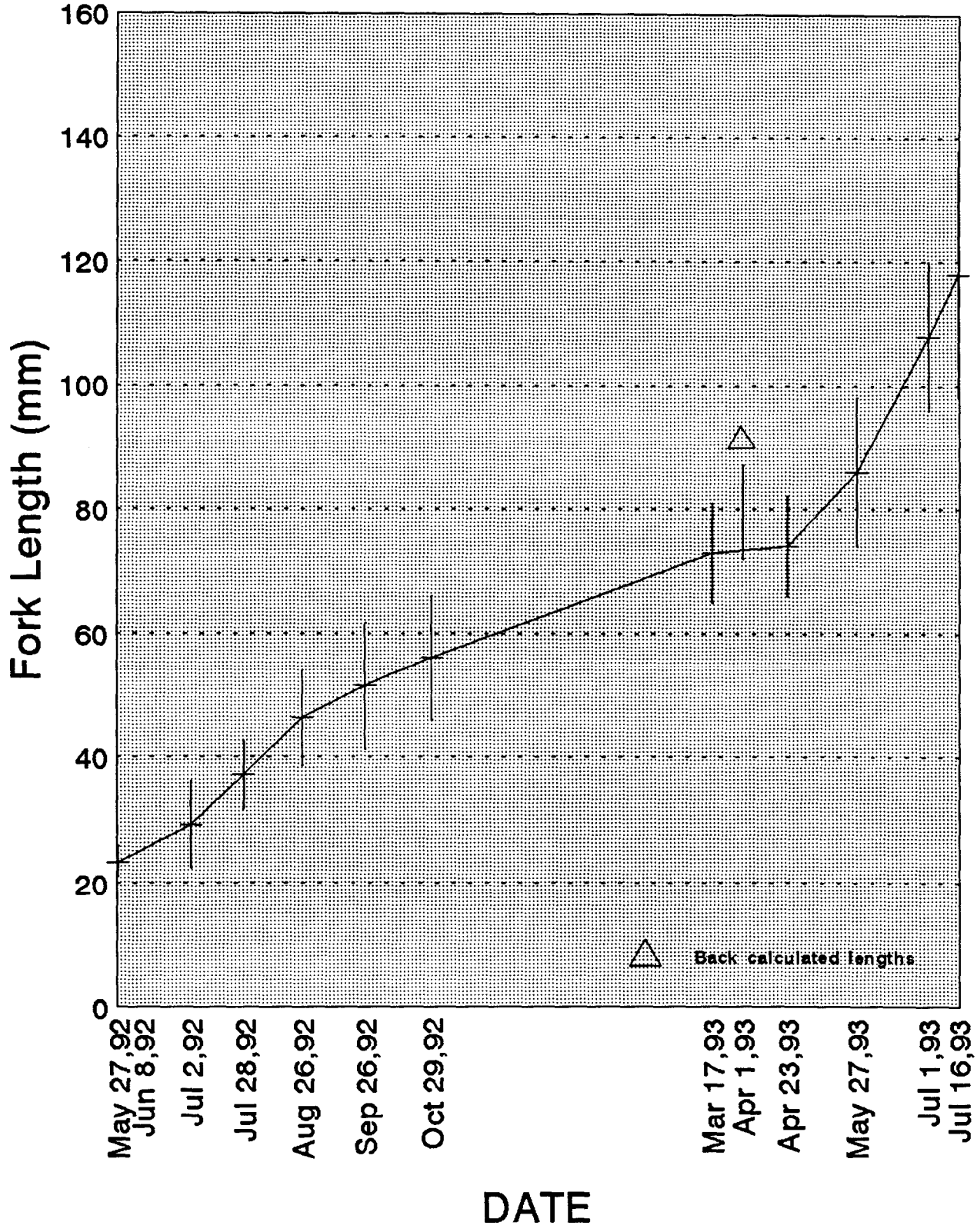

Figure 3. Observed growth curve for 1992 kokanee cohort (May 27, 1992 to July 16, 1993) plotted with back calculated mean length from four sample dates (April 23, May 27, July 1, July 16) in 1993.

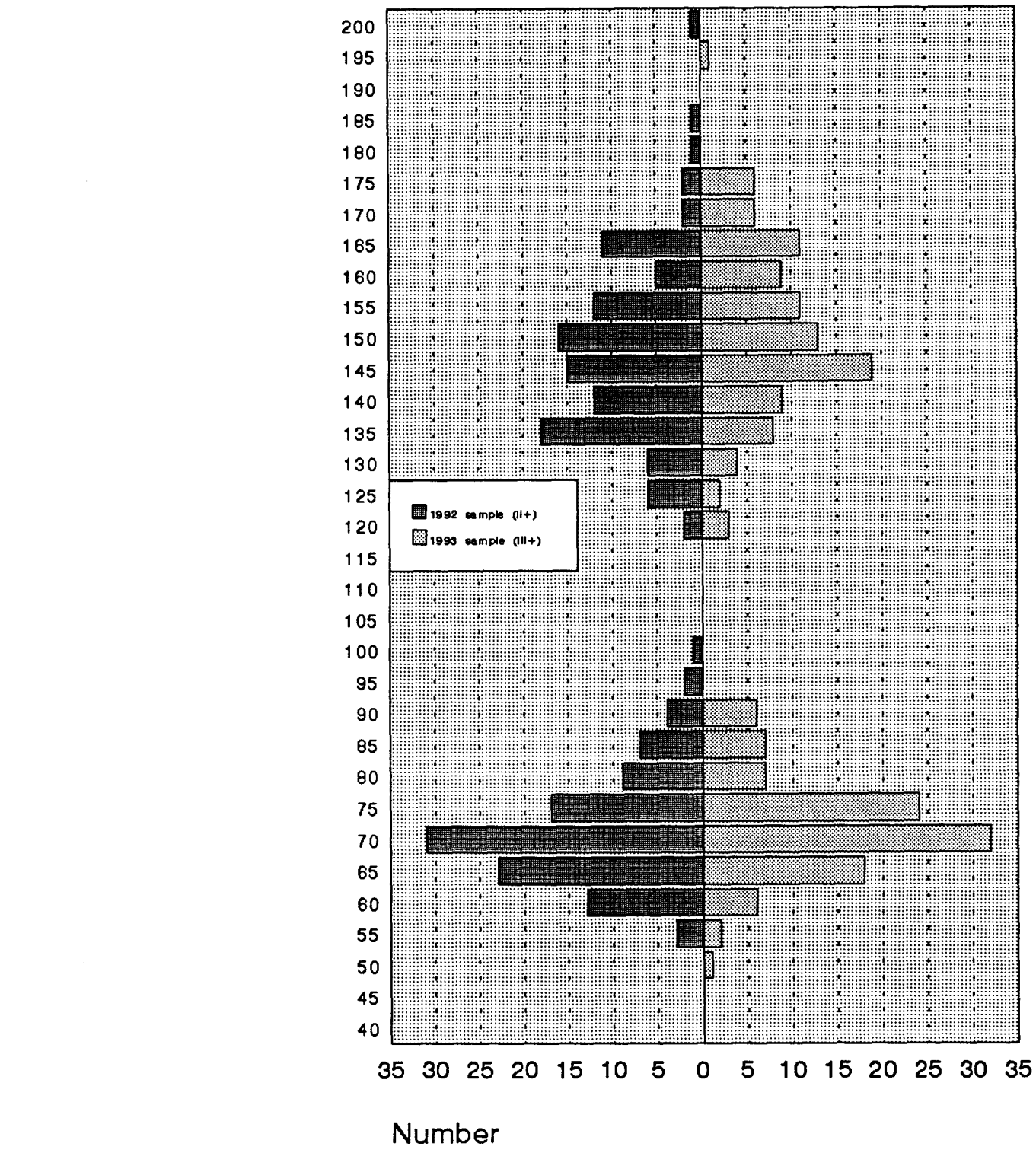

Figure 4. Kokanee fork lengths back calculated for 1990 cohort fish sampled in 1992 (left) and 1993 (right).

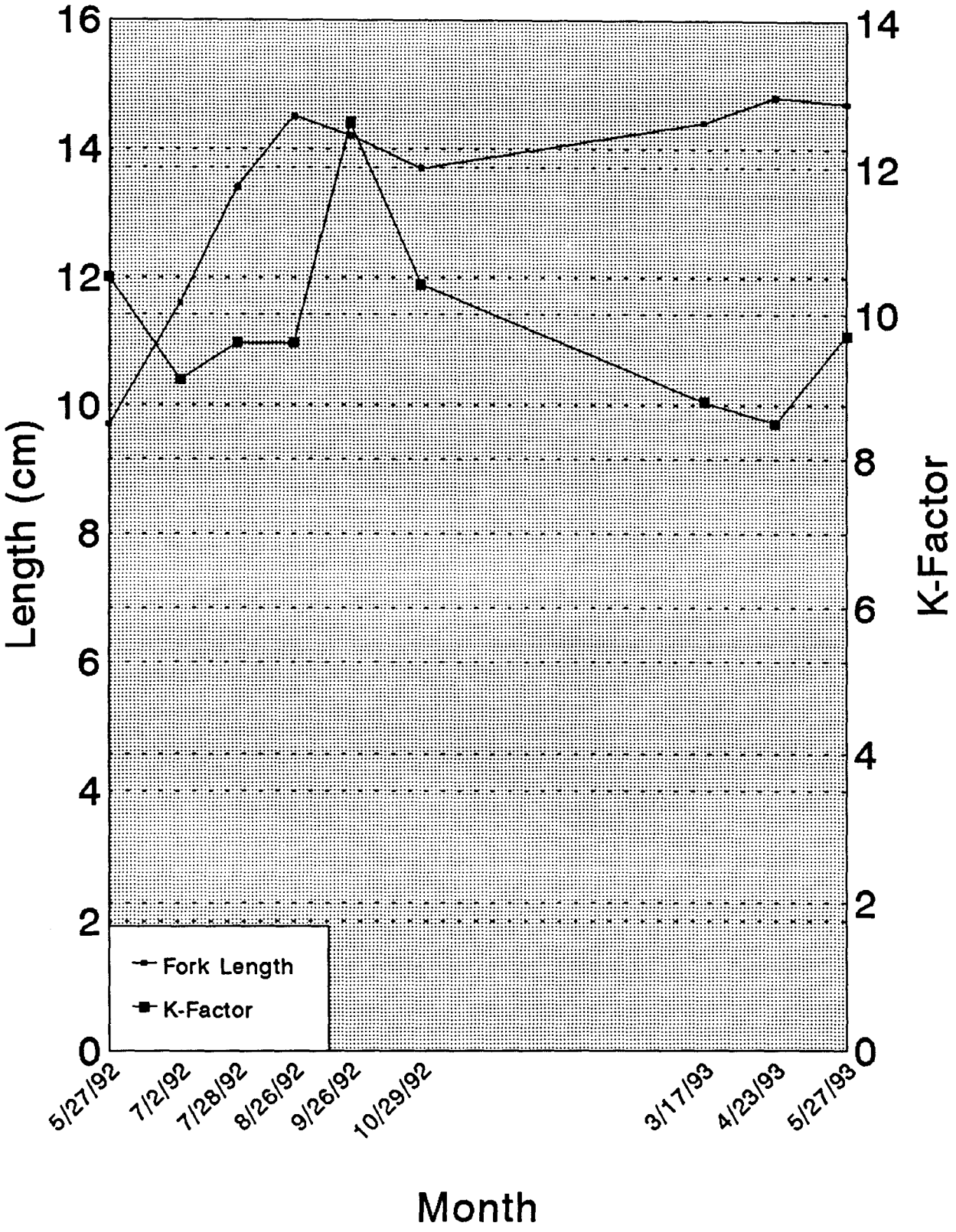

Figure 5. The 1991 kokanee cohort length increase over winter and decrease in K-factor.

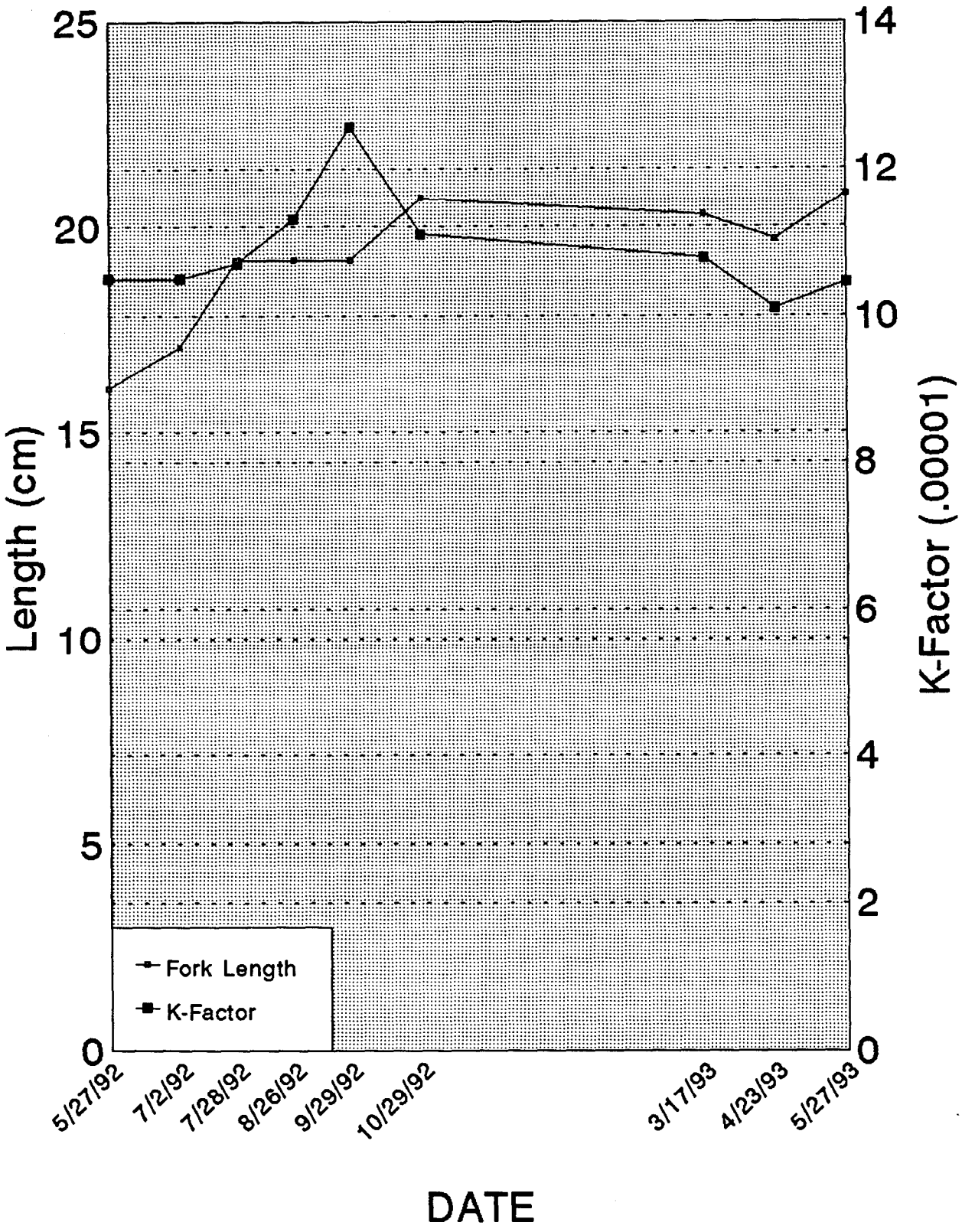

Figure 6. The 1990 kokanee cohort change in length and K-factor over the 1992/93 winter.

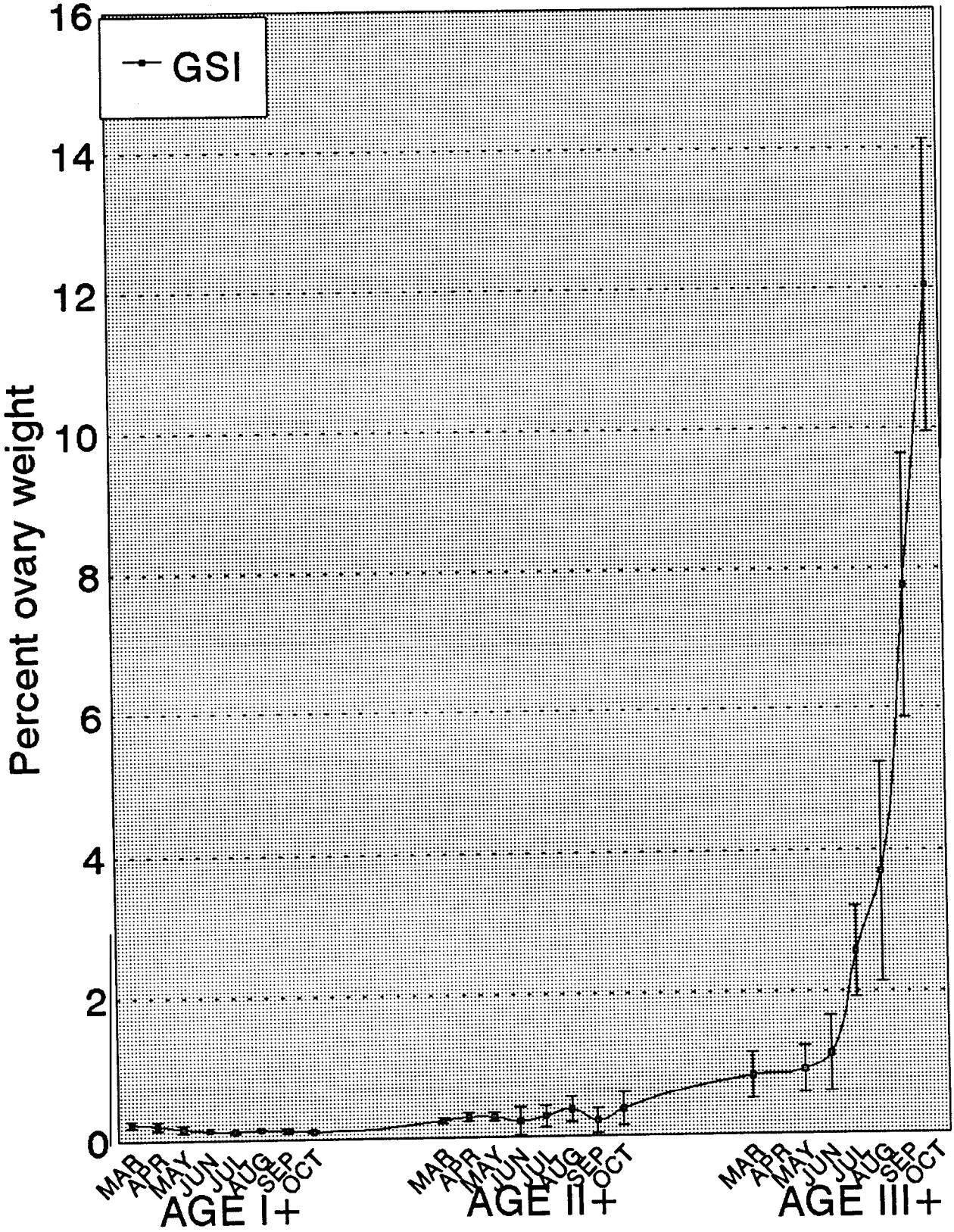

Figure 7. Gonadosomatic index for female kokanee cohorts 1990, 1991, 1992 in Coeur d'Alene Lake.

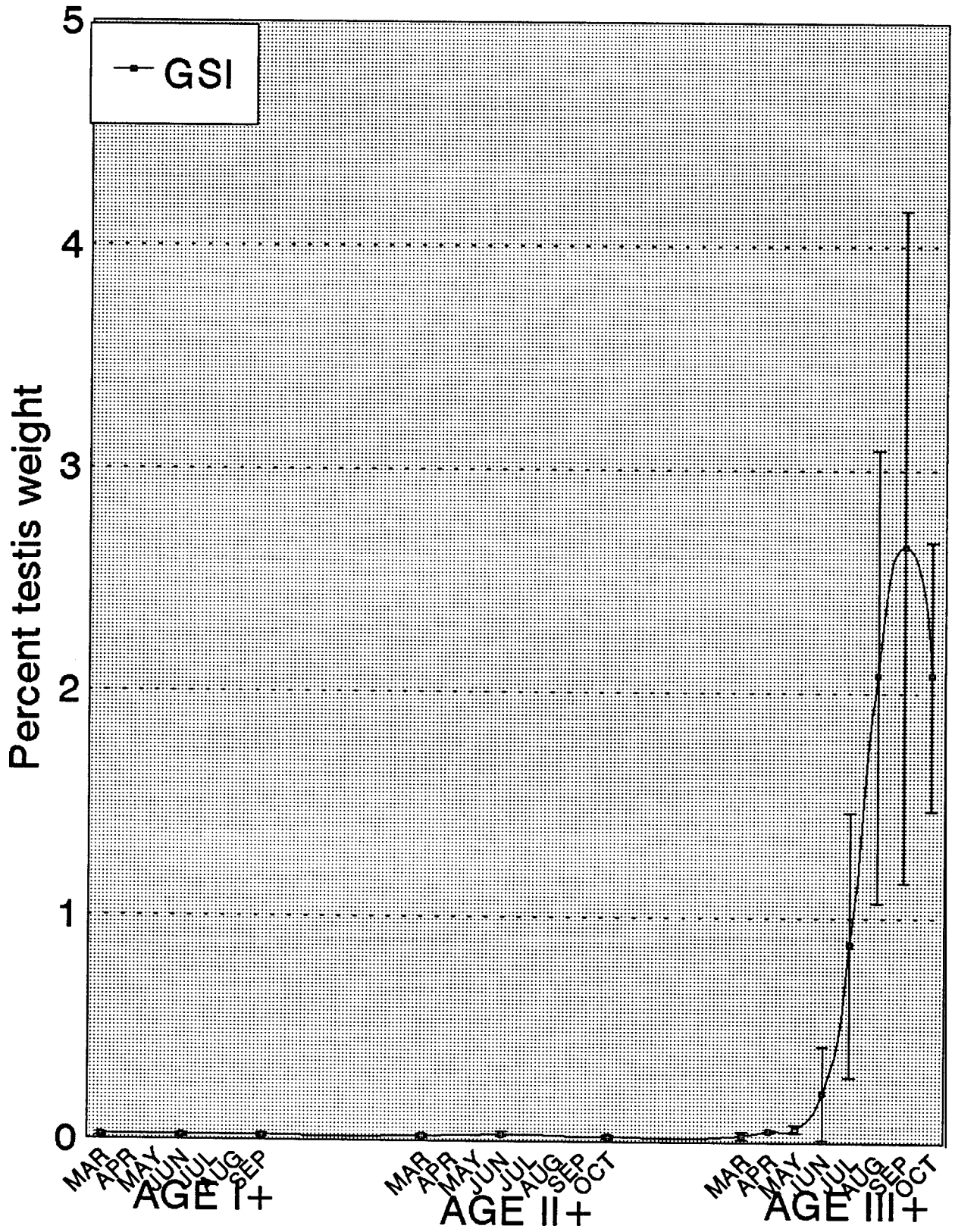

Figure 8. Gonadosomatic index for male kokanee cohorts 1990, 1991, 1992 in Coeur d'Alene Lake.

REFERENCES

Bailey, J.K., R.L. Saunder, and M.I. Buzeta. 1980. Influence of parental smolt age on growth and smolting of hatchery-reared Atlantic salmon (Salmo salar). Canadian Journal of Aquatic Sciences. 37:1379-1353.

Bagenal, T.B., and F.W. Tesch. 1978. Age and Growth. In T.B. Bagenal, editor. Methods for Assessment of Fish Production in Fresh Waters. Blackwell Scientific Publication, Oxford, 101-136.

Balinsky, B.L. 1970. An Introduction to Embryology. Philadelphia, London and Toronto: W.B. Saunders.

Bowler, B., B.E. Rieman, and V.L. Ellis. 1979. Pend Oreille Lake Fisheries Investigations. Idaho Department of Fish and Game. Federal Aid in Fish Restoration. Project F-73-R-1. Job Performance Report. Boise.

Bowles, E.C., V.L. Ellis, D. Hatch, and D. Irving. 1987. Kokanee Stock Status and contribution of Cabinet Gorge Hatchery, Lake Pend Oreille, Idaho. Idaho Department of Fish and Game. Annual Report to Bonneville Power Administration. Contract DE-A179-85BP22493, Project 85-339. Boise.

Bowles, E.C., B. Hoelscher, V.L. Ellis. 1989. Kokanee Stock Status and contribution of Cabinet Gorge Hatchery, Lake Pend Oreille, Idaho. Idaho Department of Fish and Game. Annual Report to Bonneville Power Administration. Contract DE-A179-85BP22493, Project 85-339. Boise

Brett J.R., and J.E. Shelbourn. 1975. Growth Rate of Young Sockeye, Oncorhynchus nerka, in Relation to Fish Size and Ration Level. Department of the Environment, Fisheries and Marine Service, Pacific Biological Station, Nanaimo, Britiths Columbia V9R5K6.

Bromage, N., and R. Cumaranatunga. 1987. Proceedings of the Third International symposium on the Reproductive Physiology of Fish. St. John's, Newfoundland, Canada.

Buckle, D. 1972. Some Histological Techniques Applicable to fish tissues. Symposium Zoology Society London No 30:153-189.

Buss, K. 1957. The controversial kokanee-a salmon for the lakes of northeastern United States. Pacific Fisheries Commission Special Purpose Report. p. 13.

Carlander, K.D. 1981. Caution on the use of the regression method of back-calculating lengths from scale measurements. Fisheries 6(1), 2-4.

Crandell P.A., and G.A.E. Gall. 1993. The genetics of body weight and its effect on early maturity based on individually tagged rainbow trout (Oncorhynchus mykiss). Aquaculture, 117:77-93.

Dustin, J., and R.L. Saunders. 1992. Effect of 6-, 12-, and 18-month Photoperiod Cycles on Smolting and Sexual Maturation in Juvenile Atlantic Salmon (Salmo salar). Canadian Journal of Aquatic Science. 49:2273-2280.

Forberg, K.G. 1982. Journal of Fish Biology, 20:145-154.

Francis, R.I.C.C. 1990. Back-calculations of fish length: a critical review. Journal of Fish Biology, 36:883-902.

Gardner, M.L.G. 1976. A review of factors which may influence the sea-age and maturation of Atlantic salmon Salmo salar Journal of Fish Biology. 9:289-327.

Glebe, B.D., and R.L. Saunders. 1986. Genetic factors in sexual maturity of cultured Atlantic salmon (Salmo salar) parr and adults reared in sea cages. In: D.J. Meerberg (Editor), Salmonid Age at Maturity. Canadian Special Publication Fish and Aquatic Science, 89:24-29.

Goede, R.W. 1993. Fish Health/Condition Assessment Procedures. Utah Division of Wildlife Resources. Fisheries Experiment Station, Logan.

Iwamoto, R.N., B.A. Alexander, W.K. Hershberger. 1984. Genotypic and environmental effects on the incidence of sexual precocity in coho salmon (Oncorhvnchus kisutch). Aquaculture, 43:105-121.

Kato, T. 1980. Relation between age at maturity and growth of kokanee, Oncorhvnchus nerka, in Lake Towada. Bulletin of National Research Institute of Aquaculture. 1:7-19.

Holtby, L.B. and M.C. Healy. 1986. Selection for Adult Size in Female Coho Salmon (Oncorhynchus kisutch). Canadian Journal of Fish Aquatic Sciences. 43:1946-1959.

Ishida, R., K. Takagi, and S. Arita. 1961. Criteria for the differentiation of mature and immature forms of chum and sockeye salmon in northern seas. International North Pacific Fisheries Bulletin. 5:27-47.

Lam, J.J. 1983. Environment influences on gonadal activity in fish. p 65-116. In: W.S. Hoar, D.J. Randall, and E.M. Donaldson (ed.) Fish Physiology: Reproduction. Vol. IXB. Academic Press, New York.

Lowell, R. 1993. Resident Fish Hatcheries Annual Report. Idaho Department of Fish and Game, Boise.

Maiole, M.A., G. Mauser, S. Elam, and R. Downing. 1991. Dworshak Dam Impact Assessment and Fishery Investigation. Idaho Department of Fish and Game. Report to Bonneville Power Administration. Contract No. DE-A179-87BP35167.

Maiole, M.A., and J.A. Davis. 1991. Coeur d'Alene Lake Investigations. Idaho Department of Fish and Game. Job Performance Report, Project F-71-12-15, Job No. 1-b. Boise.

Mauser, G.R., and N. Horner. 1982. Enhancement of trout in large north Idaho lakes. Idaho Department of Fish and Game, Job Performance Report, Project F-73-R-6. Boise.

Metcalfe, N.B. 1991. Competitive ability influences seaward migration age in Atlantic salmon. Canadian Journal of Zoology. 69:815-817.

Michael, E., P. Chadwick, R.G. Randall, and C. Leger. 1986. Ovarian development of Atlantic salmon (Salmo palar) smolts and age at first maturity. In: D.J. Meerburg (Editor) Salmonid age at maturity. Canadian Special Publication Fisheries and Aquatic Sciences, 89:15-23.

Nagahama, Y. 1983.The Functional Morphology of Teleost Gonads. Fish Physiology. Volume IXA. pg 223-264. Copyright Academic Press, Inc.

Newman, R.M., and S. Weisberg. 1987. Among- and within-fish variation of scale growth increments in brown trout. The Age and Growth of Fish. Robert C. Summerfelt (editor) and Gordon Hall. The Iowa State Press. Ames.

Ng, T.B., and D.R. Idler. 1983. Yolk formation and differentiation in teleost fishes. Fish Physiology. Volume IXA. pg. 373-397. Copyright Academic Press, Inc.

Paragamium, V., V. Ellis, Anderson. 1990. Kokanee Stock Status and contribution of Cabinet Gorge Hatchery, Lake Pend Oreille, Idaho. Idaho Department of Fish and Game. Annual Report to Bonneville Power Administration. Contract DE-A179-85BP22493, Project 85-339. Boise.

Paragamium, V., V. Ellis, R. Gariss. 1991. Kokanee Stock Status and contribution of Cabinet Gorge Hatchery, Lake Pend Oreille. Idaho Department of Fish and Game. Annual Report to Bonneville Power Administration. Contract DE-A179-85BP22493, Project 85-339. Boise, Idaho.

Peterman, R. 1985. Patterns of interannual variation in age at maturity of sockeye salmon (Oncorhvnchus nerka) in Alaska and British Columbia. Canadian Journal of Fish Aquatic Sciences, 42:1595-1607.

Piper, R. 1970. Know the proper carrying capacities of your farm. American Fishes and U.S. Trout News. 15(1):4-6, 30.

Refstie, T., and A. Kittelsen. 1976. Effect of density on growth and survival of artificially reared Atlantic Salmon. Aquaculture 8:319-326.

Reid, W. 1989. A Survey of 1987 Idaho Anglers Opinions and Preferences. Job Completion Report, F-35-R-13. Idaho Department of Fish and Game, Boise.

Rieman, B.E. 1977. Lake Pend Oreille limnological studies. Idaho Department of Fish and Game. Federal Aid in Fish Restoration, Project F-53-R-12, Job IV-d, Job Performance Report. Boise.

-- 1992. Personal Communication. Principle Research Biologist, Fisheries. Idaho Department of Fish and Game. Eagle.

Rieman, B.E., and C.M. Falter. 1981. Effects of the establishment of Mvsis relicta on the macrozooplankton of a large lake. Transactions of the American Fisheries Society. 110:613-620.

Rieman, B.E., and D. Myers. 1990. Status and analysis of salmonid fisheries, Kokanee Population Dynamics. Idaho Department of Fish and Game. Job Performance Report. Project F 73-R-12. Boise.

Ricker, W.E. 1938. "Residual" and kokanee salmon in Cultus Lake. Journal of Research Board of Canada. 4:192-218.

-- 1972. Heredity and environmental factors affecting certain salmonid populations, p. 19-160. In: R.C. Simon and P.A. Larkin (editor). The stock concept in Pacific salmon. H.R. MacMillan Lectures in Fisheries, University of British Columbia Press, Vancouver.

-- 1992. Back-calculation of fish lengths based on proportionality between scales and length increments. Canadian Journal of Fisheries and Aquatic Sciences, 49:1018-1026.

Rogers, D.E. 1987. The regulation of age at maturity in Wood River sockeye salmon (Oncorhvnchus nerka). In: H.D. Smith, L. Margolis, and C.C. Wood (editor) Sockeye salmon (Oncorhvnchus nerka) population biology and future management. Canadian Special Publication Fisheries and Aquatic Sciences, 96:78-89.

Rowe, D.K., J.E. Thorpe, and A.M. Shanks. 1991. Role of fat stores in the maturation of male Atlantic salmon (Salmo salar) and their hybrids. Canadian Journal of Fish Aquatic Sciences. 41: 1139-1149.

Russell, P.J. 1992. Genetics. 3rd edition. Reed College. Harper Collins Publishers.

Saunders, R.L., E.B. Henderson, B.D. Glebe, E.J. Loudenslager. 1983. Evidence of a major environmental component in determination of the grilse:larger salmon ratio in Atlantic salmon (Salmo salar). Aquaculture, 33:107-118.

Scarnecchia, D.L. 1983. Age at sexual maturity in Icelandic stocks of Atlantic salmon (Salmo salar). Canadian Journal of Fish Aquatic Sciences. 41:917-935.

Scott, A.D., and J.P. Sumpter. 1983. The control of trout Reproduction: basic and applied research on hormones, p. 176-199. In: J.C. Rankin, T.J. Pitcher and R. Duggan (editor). Control Processes in Fish Physiology. Croom Helm, London and Canberra.

Sutterlin, A.M., and D. MacLean. 1984. Age at first maturity and the early expression of oocyte recruitment processes in two forms of Atlantic salmon (Salmo salar) and their hybrids. Canadian Journal of Fisheries and Aquatic Sciences, 41:1139-1149.

Swanson, P., K. Suzuki, H. Kawauchi, W.W. Dickhoff. 1991. Isolation and Characterization of Two Coho Salmon Gonadotropins, GTH I and GTH II. Biology of Reproduction, 44:29-38.

Swanson, P. 1991. Salmon Gonadotropins: Reconciling old and new ideas. Proceeding of the fourth international symposium on the reproductive physiology of fish. A.P. Scott (editor), J.P. Sumpter, D.E. Kime, and M.S. Rolfe. Publication Fish Symposium, 91, Sheffield.

Thorpe, J.E., R.I.G. Morgan, E.M. Ottaway, M.S. Miles. 1980. Inheritance of development rates in Atlantic salmon. Journal of Fish Biology, 17:13-21.

Thorpe, J.E. and R.I.G. Morgan. 1980. Growth-rate and smolting-rate of progeny of male Atlantic salmon parr, Salmo salar. Journal of Fish Biology. 17:451-460.

Thorpe, J.E., R.I.G. Morgan, C. Talbot, M.S. Miles. 1983. Inheritance of developmental rates in Atlantic salmon, Salmo salar L., Aquaculture, 33:119-128.

Thorpe, J.E. 1986. Age of first maturity in Atlantic salmon, Salmo salar. Freshwater period influences and conflicts with smolting. In salmonid age at maturity. Edited by D.J. Meerburg. Canadian Special Publication Fisheries and Aquatic Sciences, 89:7-14.

van den Hurk, R., and J. Peute. 1979. Cyclic changes in the ovary of the rainbow trout, Salmo gairdneri, with special reference to sites of steroidogenesis. Cell Tissue Research. 199:289-306.

Wallace, R.A., and K. Selman. 1981. Cellular and Dynamic Aspects of Oocyte Growth in Teleosts. American Zoology. 21:325-343.

Wallace, R.A., K. Selman, and V. Barr. 1986. Oogenesis in Fundulus heteroclitus IV. Yolk-Vesicle Formation. The Journal of Experimental Zoology. 239:277-288.

West, G. 1990. Methods of Assessing Ovarian Development in Fishes: a Review. Australian Journal of Marine and Freshwater Research. 41(2).

Wood, C.C., and C.J. Foote. 1990. Genetic differences in the early development and growth of sympatric sockeye and kokanee (Oncorhynchus nerka), and their hybrids. Canadian Journal of Fish and Aquatic Sciences. 47:2250-2260.

Yamamato, K., H. Sayuki, K. Hisayuki and R. Ishida. 1959. A preliminary report on the formation of the egg of the trout, Oncorhynchus masou. Bull. Hokkaido Regional Fisheries Research Lab. 20.

Yan, L., P. Swanson, W.W. Dickhoff. 1992. A Two-Receptor Model for Salmon Gonadotropins (GTH I and GTH II). Biology of Reproduction, 47:418-427.

Submitted by:

Scott D. Patterson
James Congleton
Dennis Scarnecchia

Approved by:

IDAHO DEPARTMENT OF FISH AND GAME

Steven M. Huffaker, Chief
Bureau of Fisheries

Virgil K. Moore
Fishery Research Manager